

# MEIOFAUNA IN PHYTAL-BASED AND SEDIMENTARY HABITATS OF A TEMPERATE MANGROVE ECOSYSTEM—A PRELIMINARY SURVEY

JANET GWYTHYR

School of Ecology & Environment, Deakin University, Geelong, Victoria 3217, Australia  
E-mail address: janetg@deakin.edu.au

GWYTHYR, J., 2000:12:01. Meiofauna in phytal-based and sedimentary habitats of a temperate mangrove ecosystem—a preliminary survey. *Proceedings of the Royal Society of Victoria* 112(2): 137–151. ISSN 0035-9211.

The assemblage structure of meiofauna from mud and pneumatophores bearing either barnacles, algae or both these epibionts was investigated in a preliminary survey of a temperate mangrove. The abundance of the sedimentary meiofauna ( $2170 \pm 155$  individuals  $\cdot 10 \text{ cm}^{-2}$ ) was found to be similar to values reported from mangrove mud in other studies. The density of meiofauna on pneumatophores ( $52 \pm 11$  and  $39 \pm 5$  individuals  $\cdot 10 \text{ cm}^{-2}$  for pneumatophores encrusted with algae and barnacles, respectively) was shown to be less than published values for sea-grass and *Spartina*, i.e. other phytal assemblages. The taxonomic richness (of level Order and above) of the habitats was compared by means of rarefaction curves to standardise samples for abundance. Meiofauna from mud showed highest taxonomic richness, but diversity in mud was significantly lower than on pneumatophores in the algal habitat. Barnacle-encrusted pneumatophores were dominated by halacarid mites, whereas algal-covered pneumatophores supported a more even assemblage of harpacticoid copepods, halacarid mites and nematodes. Multivariate analyses using ANOSIM showed the meiofauna assemblages from the three mangrove habitats were significantly different. These findings form the basis for further studies of the meiofauna of mangrove epibionts and are discussed in the context of the small-scale physiognomy of these habitats.

*Key words:* meiofauna, mangrove, habitat, pneumatophore, sediment.

ALTHOUGH two papers by Gee & Somerfield (1997) and Somerfield et al. (1998) have examined the meiofaunal communities in Malaysian mangrove leaf litter, there have been few studies of the meiofaunal community of living mangrove structures such as trunks, branches, hanging roots and pneumatophores. These biogenic structures offer a firm, phytal surface in a benthic habitat which otherwise consists of soft mud. In only one study has the meiofauna of pneumatophores been examined, and this was for a single square metre of pneumatophores cut from the mangrove *Avicennia marina* in New South Wales (Nicholas et al. 1991). Macro-organisms such as barnacles, filamentous and thalloid algae, grow patchily upon pneumatophores but any effect that these may have on resident meiofauna is not known.

In contrast with epiphytall assemblages, sedimentary meiofaunal communities of tropical mangroves have been extensively studied. Alongi (1987a) and colleagues reported lower nematode abundances from mangroves in tropical northern Queensland than from other coastal systems around the world. In laboratory and field trials Alongi (1987b) showed that meiofaunal abundance was negatively affected by mangrove derived tannins (plant secondary metabolites), and the poor nutritional value of

mangrove detritus (Alongi & Christoffersen 1992). The use of secondary metabolites by aquatic and terrestrial plants to deter herbivores and detritus feeders is well documented (for references see Alongi 1987b). However, in a southern African estuary, Dye (1983) found that meiofaunal density was highest in samples of sediment taken within the denser parts of the mangrove forest where the highest concentrations of tannins in the sediment might be expected.

In the mangroves of temperate south-eastern Australia, sediment-dwelling meiofauna have been studied by Hodda & Nicholas (1985, 1986), Hodda (1990) and Nicholas et al. (1991). Nematode densities in New South Wales were within the range for mangroves elsewhere, but lower than those for non-mangrove estuaries (Nicholas et al. 1991). Many nematode genera and some species were found in common between tropical and temperate mangrove systems.

The correlations between physical factors in the environment and some parameters of meiofaunal populations in the Hunter River estuary were examined by Hodda & Nicholas (1985). Elevation above low tide mark, salinity, presence of algal food, depth of the reducing layer and pollution were factors that accounted for differences in

meiofauna between sites. Temporal changes in sedimentary meiofauna from the Hunter River estuary were investigated by Hodda & Nicholas (1986) and shown to be largely non-seasonal. The presence of mangroves and the mild climate were suggested to explain the contrast with seasonal fluctuations in density of meiofauna from estuaries in other parts of the world. Variation in nematode populations from three south-east Australian estuaries was further examined by Hodda (1990) who showed that stochastic changes probably caused by small scale spatial and temporal variability on food sources accounted for the largest component (35%) of the total variation.

This study aims to examine the abundance and composition of meiofauna from pneumatophores compared with sediment assemblages, within a temperate Australian mangrove forest located in Victoria by addressing the following questions.

1. Which meiofaunal taxa utilise pneumatophores of *Avicennia marina* as habitat?
2. Do these assemblages differ in their composition and abundance from sediment meiofauna?
3. Is the meiofaunal composition of a given pneumatophore related to the dominant macroepibiont growing on the pneumatophore and hence may it be predicted from these more easily visible communities?

## METHODS

### *The study site*

The study site consisted of an intertidal area measuring 60 m × 50 m, situated on the eastern bank of the Barwon estuary on the southern Victorian coast of Australia (38°17'S, 144°30'E). The tidal amplitude in the area was 1.8 m and the study site was immersed to a depth of approximately 1 m at the seaward edge at mean high tide. The site was staked out into four horizons (0–3 in Fig. 1) parallel to the shoreline and these were naturally defined by the extent of the saltmarsh, the position of the landward and seaward edges of the tree canopy and the seaward extent of the pneumatophores. The horizons were divided along the length of the study site into four transects (A–D in Fig. 1).

### *Sample collection and processing*

Samples were collected randomly from the 16 grid-cells on six dates at intervals of between two and six weeks apart over 16 months between July 1996

and November 1997. A total of 171 samples were collected, comprising 98 sediment cores and 73 pneumatophores. Each core was removed using a drinking straw of internal diameter 6 mm, which was inserted carefully and vertically into the mud to a depth of 10 mm. Pneumatophores were clipped off just above the sediment surface and transferred individually to sealable plastic bags. All samples were transferred to the laboratory and fixed in 10% formalin with Rose Bengal soon after collection. Each sediment core was washed through nested 500  $\mu\text{m}$  and 53  $\mu\text{m}$  sieves and the retained fraction then backwashed into a counting tray. This was scanned at  $\times 20$  magnification; all animals were identified to major taxon (Phylum, Class, Order) and counted. The length and diameter of each pneumatophore was recorded and percentage cover (to the nearest 10%) of algae and/or barnacles on each pneumatophore was estimated by eye. Each root was then transferred to a stoppered measuring cylinder for repeated shaking and decantation. At least five washings were made for each sample; the process was repeated until no further meiofauna were extracted. The specimens were collected onto a 53  $\mu\text{m}$  sieve and counted as described above for sediment cores.

### *Field data collection and analysis*

*Pneumatophores.* The density of pneumatophores was estimated by counting the number in 50 × 50 cm quadrats placed at 2 m intervals down a transect extending from the *Avicennia* canopy edge to the seaward extremity of any pneumatophores. Data from four transects (A–D, see Fig. 1) were recorded.

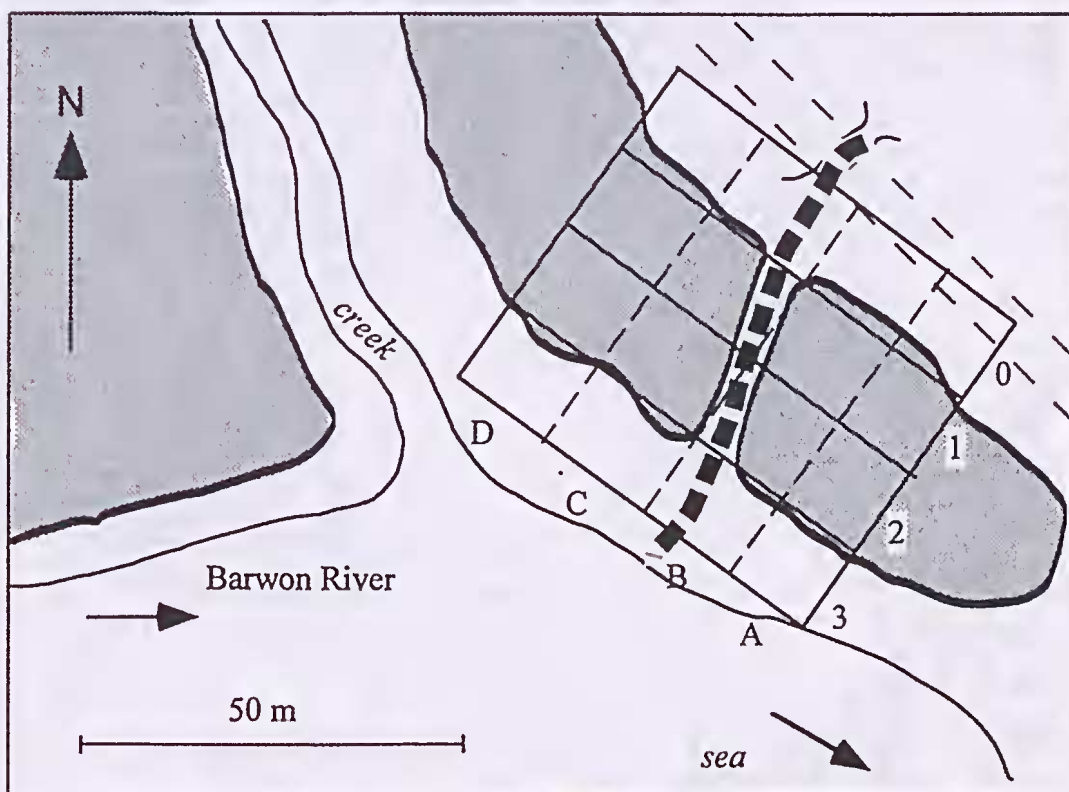
Pneumatophore surface area was derived from the formula for surface area (SA) of a cylinder ( $SA = \pi \cdot d \cdot l$ , where  $d$  is the diameter and  $l$  the length of the pneumatophore, measured using calipers). The tip area was not included due to its attenuated shape and absence of epibionts (pers. obs.) The pneumatophores provide discrete islands of solid substratum, each of which is either bare, partially or entirely covered in algae, barnacles or a combination of these epibionts. Because of their characteristics and the dominant epibionts, these phytal habitats may be described as algal, barnacle or mixed biotopes, respectively. The percentage cover of algal and barnacle epibionts on pneumatophores was estimated to the nearest 10% by eye, and multiplied by the pneumatophore surface area to estimate the total surface area of each biotope. Meiofauna in pneumatophores and sediment biotopes were expressed as numbers  $10 \text{ cm}^{-2}$ .

Data were analysed using univariate statistics within the SYSTAT and SPSS software packages and non-parametric multivariate techniques in Plymouth Routines in Multivariate Ecological Research (PRIMER; Clarke & Warwick 1994). ANOVA was used to test whether substratum type was a significant factor affecting abundances or diversity indices.

Cochran's test was used to test for homogeneity of variances (Underwood 1997), and all animal abundances were  $\log_{10}$  transformed prior to ANOVA to minimise heterogeneity.

Diversity of meiofauna sampled from mud, algal and barnacle biotope was compared using the Shannon Index, and evenness values estimated by Pielou's Index. The means of these indicators were tested between habitats by ANOVA. ANOVA and Scheffé's pairwise comparison of means was used to identify values which differed.

Taxonomic richness in each habitat was estimated using rarefaction curves generated by the ECOSIM program (Gotelli & Entsminger 1997). These curves illustrate the expected number of taxa in a small sample of individuals from each habitat, allowing



### Legend



Canopy of *Avicennia marina*



Storm water channel

Fig. 1. Plan of the study site. Horizon 0=saltmarsh vegetation; horizon 1=landward half of the canopy-shaded mudflat; horizon 2=seaward half of the canopy-shaded mudflat; horizon 3=unshaded mudflat with pneumatophores. A-B are four parallel transects within which samples were collected. Location of a drainage channel is indicated by the broad broken line.



for a comparison of the number of species in samples that have been standardised for abundance (Gotelli & Graves 1996). The rarefaction procedure, unlike other diversity measures, is based on an appropriate statistical model, is sensitive to rare taxa and unbiased by sample size (Smith & Grassle 1977).

Multivariate analyses were performed using PRIMER software on the assemblages of meiofauna from algal-covered pneumatophores, barnacle-covered pneumatophores and mud.

For the multivariate analyses counts of taxa from a total of 171 samples collected over 16 months from the same substratum type on the same date and from the same grid-cell within the study-site were pooled, to give 27 mean values. These mean abundances from each set of replicate samples were used in construction of a Bray-Curtis similarity matrix, after double square root transformation. Ordination of the sample means from the similarity matrix was by non-metric Multi-Dimensional Sealing (MDS; Clarke & Green 1988). Statistical differences among *a priori* validity of the apparent

groups was tested using the ANOSIM permutation test (Clarke 1993), where the null hypothesis was that no significant differences existed among the similarities of meiofauna assemblages from the three biotopes.

The contribution of each species to the average Bray-Curtis dissimilarity between pairs of groups was computed using the similarity percentages procedure (SIMPER; Clarke 1993). The average similarity within a group is also calculated by this PRIMER module.

The relationship between abundance of fauna and the interval between sampling dates was examined using the RELATE module of PRIMER, which is a permutation test for examining the lack of relationship between any two similarity matrices. This test discerns temporal trends when a date matrix is compared with the abundance similarity matrix.

Association between sampling sites and abundance of taxa was also investigated using RELATE, where the second matrix was computed from a two-dimensional spatial layout of the 16 grid cells within the study site.

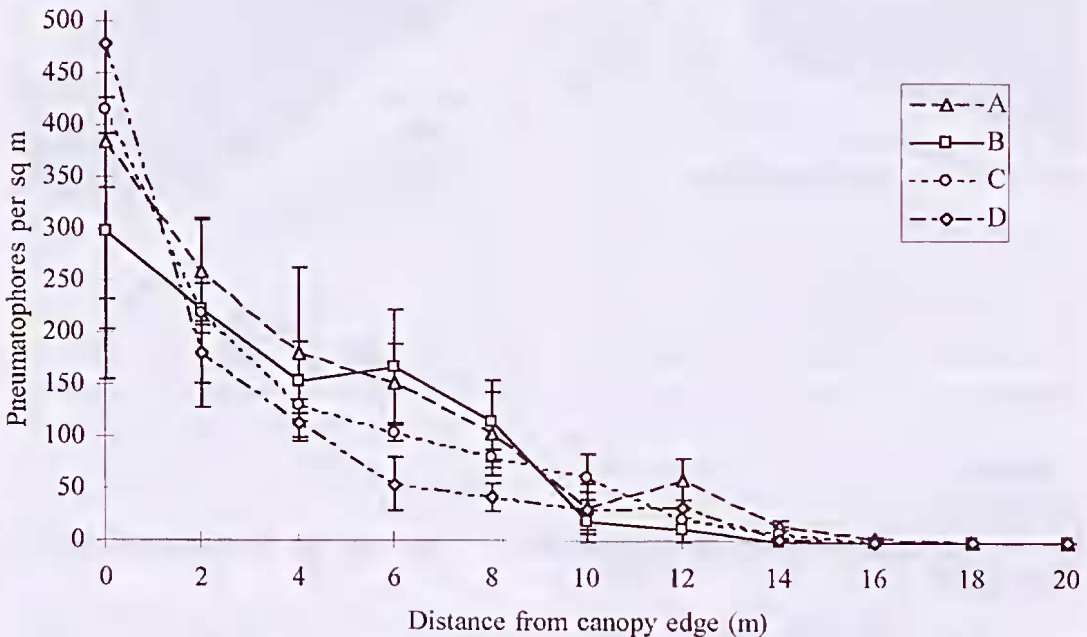


Fig. 2. The density of pneumatophores along four transects in the Barwon estuary. The mean density and standard error of densities from three quadrats at each point is shown. Transects A-D were approximately 20 m apart; for location refer to Fig. 1.

RESULTS

Availability of substrate

The highest density of pneumatophores occurred under the canopy of *Avicennia* trees and decreased with distance down the shore from the trees (Fig. 2). The available area of algal- and barnacle-covered habitat was derived from the percentage cover of each epibiont, the density of pneumatophores per square metre and their surface area. Results for each transect are presented in Fig. 3. Pneumatophores under the tree canopy and at the seaward edge bore sparse epibionts compared with pneumatophores between these boundaries. Barnacles generally occupied more primary space on pneumatophores than algae. The epibiont

coverage on any pneumatophore was generally dominated either by algal growth or barnacles. Only 6 pneumatophores from 73 sampled were estimated to have about 50% coverage of each biotope.

The total abundance of meiofauna in each habitat

The mean overall abundances of all animals from each different habitat are shown in Table 1A. The abundance of animals from mud samples was significantly greater than from an equal area of pneumatophore biotope.)

Although no differences were detected between transects (Table 2A), there was a significantly

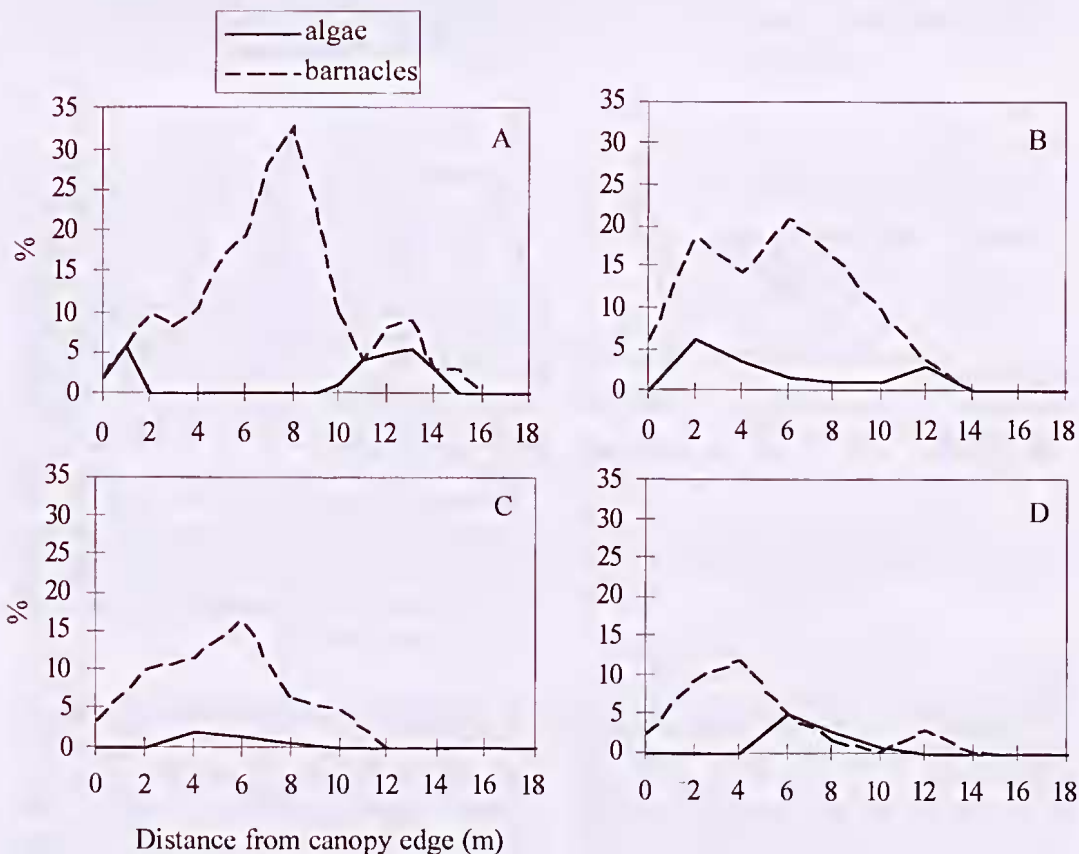


Fig. 3. The percentage area of algal- and barnacle-covered pneumatophores relative to the area of sediment, along transects A-D.

A.			
Habitat	Mean abundance (individuals 10 cm <sup>-2</sup> )	Standard error	No. of samples
Mud	2170 <sup>a</sup>	155	98
Pneumatophores with algae	52 <sup>b</sup>	11	25
Pneumatophores with barnacles	39 <sup>b</sup>	5	40

B.				
Source of variance	df	Mean-square	F-ratio	p
Substrate	2	325.753	442.857	<0.001
Error	160	0.736		

Table 1. A. The abundance of meiofauna (all taxa) from intertidal mangrove habitats in the Barwon estuary. Common superscripts identify the abundances which do not differ significantly. B. Analysis of variance of total abundance (log number of individuals 10 cm<sup>-2</sup>) of meiofauna in different habitats.

A.						
Substrate	Mean density meiofauna 10 cm <sup>-2</sup> of substrate in Transect:				F	p
	A	B	C	D		
Mud	2000	2558	2260	1986	0.859	0.465
Pneumatophores with algae	62	53	111	29	2.925	0.058
Pneumatophores with barnacles	47	31	20	14	0.499	0.685

B.						
Substrate	Mean density meiofauna 10 cm <sup>-2</sup> of substrate in Horizon:				F	p
	0	1	2	3		
Mud	2135	2750	1736	2162	1.050	0.374
Pneumatophores with algae	24	74	22	49	1.910	0.159
Pneumatophores with barnacles	na	1.4	46	39	13.137	<0.001

Table 2. The mean abundance and results of one-factor ANOVA of all meiofauna contrasting the transects (A) and horizons (B) of the study site. See Fig. 1 for details of the locations. na = No barnacle-fouled pneumatophores were present in Horizon 0.

lower number of meiofauna from barnacle-covered pneumatophores on the landward half of the tree-shaded zone (horizon 1) compared with under the seaward side of the canopy (horizon 2), and the exposed mudflat (horizon 3), as shown in Table 2B.

The combined totals of meiofauna from pneumatophores and sediment are shown in Fig. 4.

The relative contribution of the pneumatophore-dwelling meiofauna as a percentage of the total abundance from sediment and pneumatophores averaged over the 16-month sampling period was examined. Because there was no significant difference between the abundance of meiofauna on algal- or barnacle-covered roots (see Table 1B), the combined average abundance of meiofauna 10 cm<sup>-2</sup> of pneumatophore was used to estimate the density of meiofauna from the pneumatophore surface area available per square metre of sediment. This overall meiofaunal density on pneumatophores of 45 individuals 10 cm<sup>-2</sup> was used with the estimates of surface area and density to yield an estimated value of 13 phytal-dwelling meiofaunal animals 10 cm<sup>-2</sup> of sediment.

#### Composition of meiofaunal assemblages

Sedimentary and phytal habitats were found to differ in coarse taxonomic composition (Table 3) as well as in total abundance of meiofauna, as described above. Nematodes were the dominant taxon in mud, representing 87% of the total organisms collected in sediment samples, with polychaetes and copepods comprising respectively 6% and 4% of the total. In phytal samples nematodes accounted for 40% of the meiofauna from algal biotope, with halacarid mites being the second most abundant taxon (31%). Pneumatophores bearing barnacles showed the least even assemblage (Table 3) in which 91% of the meiofauna was halacarid mites, with copepods representing a further 7% of the total. Nematodes comprised only 1% of the animals from the barnacle biotope. Only halacarids were found living on bare pneumatophores.

#### Diversity of meiofaunal assemblages in different habitats

Table 4A shows the Shannon diversity index and Pielou's evenness index for meiofaunal communities from mud, algal and barnacle habitats. The distributions of the populations of H' and J values satisfied normality requirements, although variances between substrates were not homogenous.

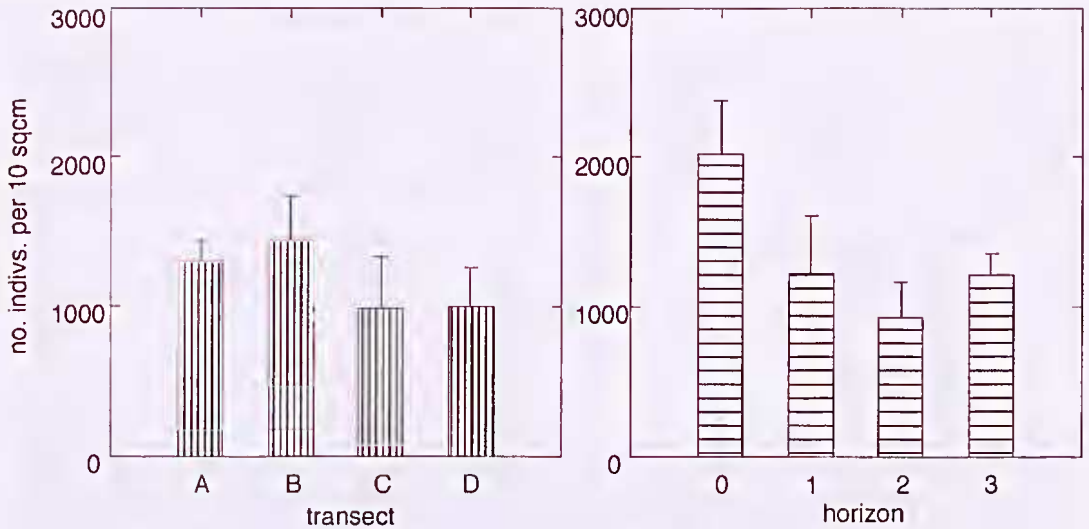


Fig. 4. The mean abundance ( $\pm$  standard deviation) of total meiofauna from mud and pneumatophores, within the study site. Horizon 0 = saltmarsh; horizons 1 and 2 = landward and seaward side of the canopy, respectively; zone 3 = mudflat. Transects A–D are adjacent strips running from the saltmarsh to the seaward limit of the pneumatophores (see Fig. 1 for details). Total  $n = 171$  samples.

Taxon	Mud	Alg	Barn	Alg/barn	Bare	Total individuals counted
Nematoda	86.5	40.1	1.1	4.7	0	6161
Copepoda	3.8	16.6	7.4	24.5	0	1492
Halacarida	0.2	31.2	90.7	69.1	100	7073
Polychaeta	5.5	0.6	0.1	0.1	0	326
Oligochaeta	0.3	0.6	0.0	0.0	0	82
Dipteran larvae	0.3	5.1	0.8	1.6	0	238
Kinorhyncha	1.4	0.0	0.0	0.0	0	77
Turbellaria	1.0	4.4	0.0	0.0	0	193
Cnidaria	1.0	0.0	0.0	0.0	0	56
Sum	5540	3091	5583	1453	31	15 698
No. samples	98	25	40	6	2	171

Table 3. The percentage composition and total numbers of meiofauna in sediment and phytal samples. Alg = pneumatophores with algae; Barn = pneumatophores with barnacles; Alg/barn = pneumatophores with algae and barnacles; Bare = pneumatophores without epibionts.

ANOVA was used to compare each index between habitats (Table 4B) and significantly different means were tested by a Tamhané *post hoc* test, which does not assume homogenous variances. Table 4B shows there were significant differences between the assemblages for both Shannon diversity and Pielou evenness indices. Highest diversity was displayed by meiofauna from algal habitat, followed by barnacle habitat, with lowest diversity present

in mud. Pielou's evenness index revealed that both epibiont-based assemblages of meiofauna were more even in their community composition than sediment meiofauna ( $p < 0.001$ ). There was no difference between evenness of algal and barnacle biotopes ( $p = 0.943$ ).

Rarefaction curves for each habitat are shown in Fig. 5. In small samples the richest assemblage was from pneumatophores bearing algae (Fig. 5A).



A.					
Habitat	Mean H'	Standard deviation	Mean J	Standard deviation	No. of samples
Mud	0.562 <sup>a</sup>	0.302	0.475 <sup>a</sup>	0.199	87
Alg	1.304 <sup>b</sup>	0.216	0.707 <sup>b</sup>	0.129	25
Barn	1.036 <sup>c</sup>	0.194	0.689 <sup>b</sup>	0.147	40
B.					
	Source of variance	df	Mean-square	F-ratio	p
H'	Between groups	2	6.733	96.338	<0.001
	Within groups	149	6.989 × 10 <sup>-2</sup>		
	Total	151			
J	Between groups	2	0.913	29.196	<0.001
	Within groups	149	3.127 × 10 <sup>-2</sup>		
	Total	151			

Table 4. A. Shannon Index (H') and Pielou's evenness index (J) values for communities from the sediment (Mud) and from algal-covered (Alg) and barnacle-covered (Barn) pneumatophores. Common superscripts identify means within each set of indices which do not differ significantly. B. ANOVA results for Shannon diversity and Pielou evenness indices between mud, algal and barnacle habitats.

A collection of just 20–30 individual meiofauna organisms from the algal biotope would be expected to include five taxonomic groups at the level of order, class or phylum. The taxonomic richness of small samples (i.e. 30 animals) from mud, pneumatophores with both epibionts and pneumatophores with barnacles is lower than (but not outside the 95% confidence limits of) the value for algal biotope. Lowest species richness was from bare pneumatophores from which only one taxon (halacarid mites) was collected.

The curve for taxonomic richness (at the level of order and above) in the mud habitat crossed the asymptote reached in the mixed biotope at a sample size of approximately 18 animals (Fig. 5A), showing that the expected richness of these two habitats depended on the abundance being compared. Fig. 5B shows continuing increase of taxonomic richness of the mud assemblage in samples of up to approximately 1000 animals, when the observed richness stabilised at almost nine taxa at the level of order, class or phylum. Assessment of between 200–1450 animals from every habitat indicated that mud was significantly more taxon-rich than any epibiont assemblage, and that meiofauna from the algal biotope was richer than that from either the barnacle or mixed epibionts. Curves for the two latter assemblages

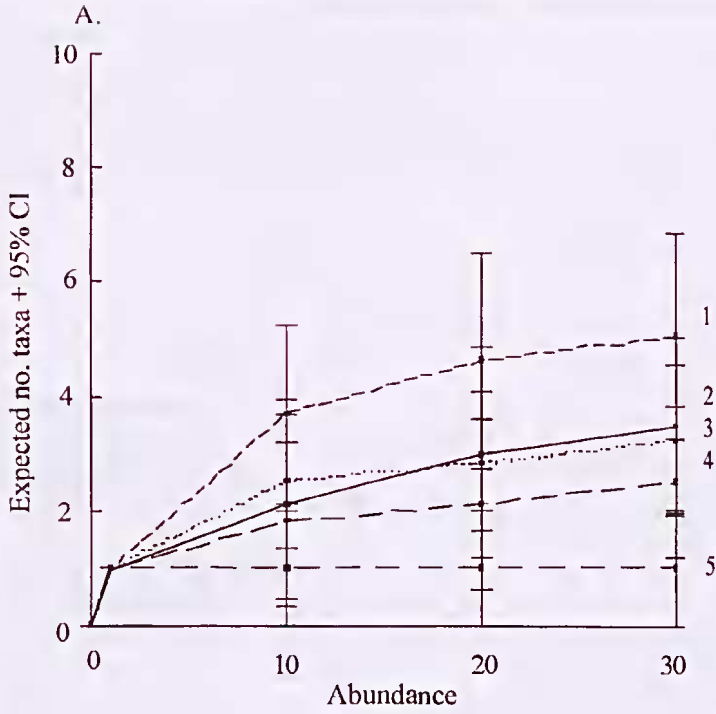
levelled out at five taxa from 1450 animals.

Multidimensional scaling (Fig. 6) showed that the phytal and sedimentary communities fell into broadly different groups. The ANOSIM procedure indicated a significant difference between both types of pneumatophore community and the sediment community (Global  $R=0.670$ ; sample  $R=0.663$ ,  $p<0.001$  for algal versus mud biotopes;  $R=0.929$ ,  $p<0.001$  for barnacles versus mud biotopes), but not between the samples from pneumatophores with algae and those with barnacles ( $R=0.298$ ,  $p=1.0$ ).

The contributions of the most discriminatory taxa found in the mangroves are shown in Table 5. The meiofauna from algal and barnacle biotopes showed more dissimilarity to each other (i.e. average dissimilarity 38%) than either of these assemblages did to the mud community (57% and 68%, respectively). The more common occurrence of nematodes on algal rather than barnacle biotopes accounted for the single greatest contribution to the dissimilarity between the two pneumatophore habitats (21%). Although nematodes favoured mud above either phytal habitat and represented 87% of the meiofauna sampled from the sediment, halacarid mites were the most discriminating taxon between either of the habitats within epibionts and mud.

Fig. 5. Rarefaction curves for the number of taxa (at the level of Order or above) and the 95% Confidence Interval (CI) from mangrove habitats. A. Samples of less than 30 animals. B. Samples of up to 1450 animals. Curves were generated using the ECOSIM program (Gotelli & Entsminger 1997).





Substrates

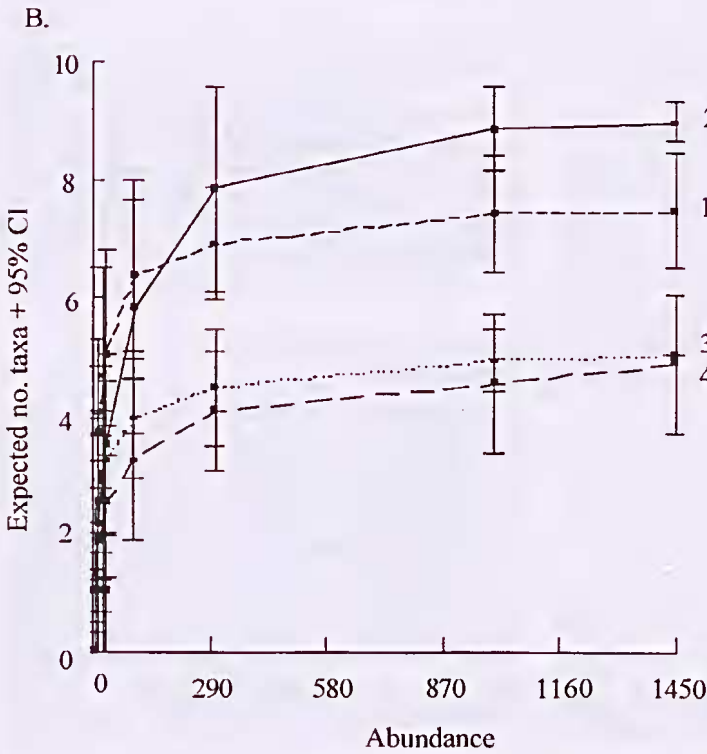
1 = pneumatophores with algae

2 = mud

3 = pneumatophores with algae & barnacles

4 = pneumatophores with barnacles

5 = bare pneumatophores



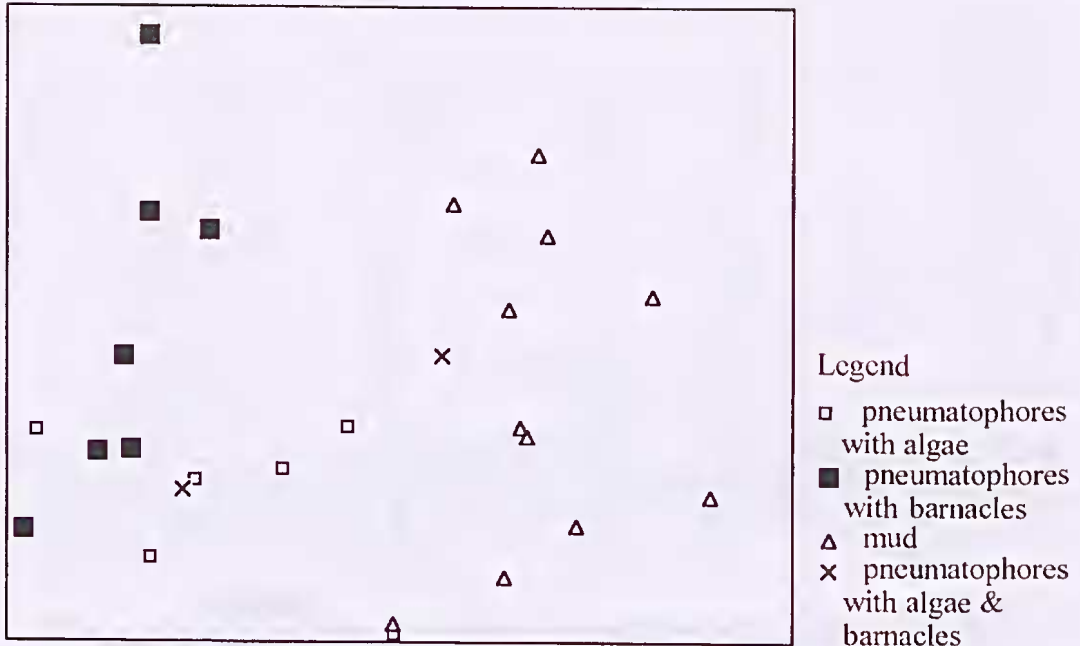


Fig. 6. MDS ordination plot (based on Bray-Curtis similarity matrix) of communities of meiofauna from different habitats. Stress = 0.11. Distance on the graph between any pair of points is proportional to the dissimilarity between the samples in terms of taxonomic composition and relative abundances.

#### *Temporal and spatial patterns of meiofauna in the survey*

No seasonal trend in abundance of the high level taxa within the 16-month duration of this survey was demonstrated, since no significant associations were found between abundance and temporal sequence matrices (1000 permutations of data in RELATE module gave Spearman's Rho of 0.002, significance 44.5%). The effect of grid position on the total abundance of animals from all substrata was found to be insignificant (1000 permutations gave a Spearman's Rho of  $-0.193$ , significance level 100%)

## DISCUSSION

#### *Sedimentary meiofaunal assemblages from mangrove habitats*

The average density of meiofauna from mud in the Barwon estuary study site was  $2.17 \times 10^3$  individuals  $10 \text{ cm}^{-2}$ , a value that concurs with meiofaunal densities from elsewhere, as shown in Table 6. Studies have described the negative influence of mangrove tannins (Alongi 1987b) as

well as enhancement of meiofauna abundance in the vicinity of fine mangrove roots (Nicholas et al. 1991). This range of responses suggests that the relationship between meiofauna and mangrove roots, their metabolic products and decaying mangrove detritus, is complex. Whether the presence of rootlets in the sediment modifies either physically or chemically the effects of noxious plant metabolites is not known.

#### *Meiofaunal assemblages from mangrove pneumatophores*

The abundance of meiobenthos on pneumatophores was similar for the algal ( $52$  individuals  $10 \text{ cm}^{-2}$ ) and barnacle ( $39$  individuals  $10 \text{ cm}^{-2}$ ) epibiont assemblages, but these were sparsely populated compared with the sediment. There are no published estimates of abundance for meiofauna from pneumatophores with which present values may be compared. Because the abundances of these two assemblages were not significantly different, their mean value of  $4.5 \times 10^4$  individuals  $\text{m}^{-2}$  was used here to represent the average density of meiofauna  $\text{m}^{-2}$  of pneumatophore surface, for comparison with other epibiotic assemblages.

However, comparison with published values is problematical because of the different ways in which the substratum is quantified between studies. When expressed as  $m^{-2}$  of algal-bearing rock surface, densities of nematodes associated with a belt of *Cladophora-Pilayella* macroalgae in Finland (Jensen 1984) were given as up to  $5 \times 10^6$  individuals  $m^{-2}$ . Values from papers listed in

Hicks (1986) range from  $1.0 \times 10^4$  to  $3.1 \times 10^6$  individuals  $m^{-2}$  for algal-dwelling communities. The densities of meiofauna on pneumatophores in the present study fall within, but at the lower end of, this range. Rutledge & Fleeger (1993) sampled meiofauna from the saltmarsh cordgrass *Spartina alterniflora* in the northern Gulf of Mexico and found a mean density of approximately 1500 individuals  $100\text{ cm}^{-2}$  of grass surface in monthly samples over one year. The average density of meiofauna on pneumatophores in the present study was 450 individuals  $100\text{ cm}^{-2}$  of pneumatophore surface, only about one-third as dense as the meiofauna living within *Spartina* assemblages. By taking the size, density and percentage cover of pneumatophores into account, the average number of meiofauna in the pneumatophore habitat at Barwon Heads expressed on a per sediment-surface basis was only 13 individuals  $10\text{ cm}^{-2}$  of sediment. Rutledge & Fleeger (1993) converted their values for the density of stem-dwelling meiofauna into the equivalent abundance expressed per unit area of sediment, giving 225 individuals  $10\text{ cm}^{-2}$ . The relative availability of vertical *Spartina* habitat (a tall, dense grass) was clearly a factor in contributing to their higher estimate of meiofaunal density.

Taxon	Per cent of dissimilarity	Cumulative %	Favoured biotope
<b>A.</b>			
Nematodes	21	21	algal
Copepods	17	38	algal
Halacarids	13	51	barnacle
Dipteran larvae	12	63	algal
Amphipods	11	74	algal
<b>B.</b>			
Halacarids	24	24	algal
Copepods	13	37	algal
Dipteran larvae	12	49	algal
Nematodes	12	61	mud
<b>C.</b>			
Halacarids	31	31	barnacle
Nematodes	19	49	mud
Polychaetes	10	59	mud
Copepods	8	68	barnacle

Table 5. Summary of the SIMPER analysis to show taxa which contribute most to the dissimilarity between pairs of communities. Favoured biotope was indicated by higher abundance. A. Algal- and barnacle-covered pneumatophores. Average dissimilarity = 38%. B. Mud and algal-covered pneumatophores. Average dissimilarity = 57%. C. Mud and barnacle-covered pneumatophores. Average dissimilarity = 68%.

*Composition and diversity in epibiotic microhabitats*

Fouling organisms increase the surface area, rugosity and complexity of the pneumatophore surface, and therefore may provide a relatively buffered microclimate particularly during emersion at low water. However, differences in the composition of the meiofauna between different epibionts point to finer resolution of the biotope than this. Copepods were significantly more likely to be found within algal habitats than

Locality	Latitude	Nematodes $\times 10^3, 10\text{ cm}^{-2}$	Total meiofauna $\times 10^3, 10\text{ cm}^{-2}$	Author
Vic., SE Australia	38°S	Mean 1.791 Range 0.050–6.850	Mean 2.170 Range 0.250–8.622	Gwyther (present study)
NSW, SE Australia	36°S	0.88	—	Nicholas et al. (1991)
NSW, SE Australia	32°S	0.063–11.892	—	Hodda & Nicholas (1985)
Transkei, S. Africa	31°S	—	$1.0 \times 10^3$ indivs $100\text{ cm}^{-3}$	Dye (1983)
Qld, NE Australia	19°S	0–2.117	—	Alongi (1990)
Kenya	4°S	1.2	—	Schrivers et al. (1995)
South Andaman	12°N	—	1.84 (max.)	Rao (1986)
India	19°N	—	2–6	Goldin et al. (1996)

Table 6. Published estimates of the abundance of meiofauna in mangrove sediments. — = no estimate given.



among barnacles; conversely, halacarid mites were more prevalent on barnacles than on algae. The habitats offered by the dominant macro-epibionts of pneumatophores clearly support characteristic assemblages of meiofauna, and these in turn are quite distinct from the mud community. No seasonal trend in abundance of the high level taxa was discernible within the 16-month duration of this survey, although it is likely that the communities may have shown seasonal changes in feeding type composition. This possibility is presently being investigated in a further study of the Barwon estuary. Temporal changes in nematode communities have been attributed by Rudnick et al. (1985) to seasonal changes in food supply, although Alongi (1990) reasoned that temperature was the most likely factor.

Jensen (1981) suggested that temporal changes in diversity of phytal nematodes could be explained by seasonal movements of nematodes between sediments and phytal habitats. However, Bell et al. (1984) pointed out that the composition of phytal and sedimentary assemblages of meiobenthos are quite distinct. In a Malaysian mangrove system, Somerfield et al. (1998) demonstrated that the meiofaunal communities in leaf litter were distinctly different from those in the sediment under *Rhizophora* trees, although no species of nematode was found exclusively on mangrove litter. The distinctive assemblages of coarse taxonomic groupings from phytal and sedimentary habitats in the Barwon estuary support those findings.

The meiofauna of barnacle-encrusted roots was dominated by halacarid mites (91% of the total number of meiofauna) and the mud by nematodes (87% of the total). These two taxa accounted for 49% of the relatively large dissimilarity between meiofauna from these two habitats. However, the coarse taxonomic composition of the meiofaunal assemblage on algae-bearing pneumatophores showed greater evenness than the assemblage from within either of the other two habitats, and the algal-dwelling assemblage was consequently more diverse (Table 4). Species richness of meiofauna from mud was significantly higher than from any of the phytal habitats (Fig. 5B), but the diversity of the mud assemblage was significantly lower than within algal habitat (Table 4B). Meiofauna from barnacles showed the lowest diversity of the epibiont assemblages.

#### *Characteristics of mangrove habitats*

Although comparisons between the diversity of assemblages cannot be made with other studies that use a different taxonomic resolution, it is valid to

make comparisons among certain characteristics of the habitats in the present study.

Species richness of meiofauna from mud was significantly higher than from any of the phytal habitats (Fig. 5B), but the diversity of the mud assemblage was significantly lower than within algal habitat (Table 4B). Meiofauna from barnacles showed the lowest diversity of the epibiont assemblages.

Habitat complexity relates to small scale attributes of habitat physiognomy (Hicks 1986) and these are distinctive between the algal- and barnacle-covered substratum. Algal cover consisting of filaments, fronds and divided thalli are provided by *Enteromorpha*, *Ulva* and *Caloglossa*, respectively, and the greater diversity of algal-associated meiofauna may be due to this topographic complexity of the surface for living on and sheltering within. Algae may provide more refuge against desiccation at low tide than is available within the interstices of barnacles. Empty barnacle tests may provide some refugia, but dead barnacles were rarely found on the pneumatophores. Protection from sun, wind and rain would seem to be less effective on the barnacle surface than within an algal canopy. The fractal dimensions of the algal epiphytes on pneumatophores exceed those of the barnacle biotope (pers. obs.) for meiofauna, and this is reflected in the relative diversity (but not in the density) of assemblages. The use of fractals as an ecologically meaningful measure of habitat complexity was discussed and developed by Gee & Warwick (1994), who revealed the relationship between high fractal dimensions of macroalgae and diversity of an epifaunal community.

The nature of the surficial layer partly depends on the prevailing hydrodynamic regime. In sheltered environments the phytal surface may develop a layer of sediment: Hicks (1986) points out that under reduced silt-clay or detrital loads, harpacticoids usually dominate algal meiofaunas, whereas silt-accumulating surfaces are dominated by nematodes. Nematodes were poorly represented on pneumatophores compared with the abundance of this ubiquitous group in the mud where they comprised 87% of the total sediment meiofauna (Fig. 5). Nematodes represented 40% of the meiofauna from algal-covered pneumatophores and only 1% of the assemblage found on barnacle-fouled pneumatophores. Investigations into phytal meiofauna in the North Sea and Chile (Hicks 1985) showed certain groups of nematodes to be dominant in phytal habitats and Somerfield & Jeal (1996) included nematodes among a list of phytal meiofauna in descriptions of the microhabitats

offered within clumps of macroalgae in Ireland. The relationship between the architecture (size and structural variety) of algal habitat and the diversity of epifaunal communities has been demonstrated by Jarvis & Seed (1996) for meiofaunal assemblages from the algae *Ascophyllum* and *Polysiphonia*. A study of ostracods from intertidal algae (Hull 1997) provided strong evidence that the degree of substrate complexity affected both the abundance and diversity of the assemblage in both space and time.

The presence of detritus on pneumatophores seemed to promote nematode abundance. This effect could reflect provision of extra food resources or favourable mechanical properties of the medium for mobility of these animals. The locomotory mode of nematodes depends on close contact of sufficiently resistant surrounding particles with the body surface: this provides forces antagonistic to longitudinal muscle contractions (nematodes lack circular musculature) and results in forward propulsion. However, in a study of the meiofauna of *Ascophyllum* in north Wales, United Kingdom, Jarvis & Seed (1996) found no significant correlations between sediment load and abundance of major taxa. Whereas copepods and nematodes occurred to some degree in all habitats, the halaearid mites were the dominant taxon of meiofauna on barnacle-covered pneumatophores but rarely found in sediment. These animals were extremely tenacious and apparently tolerant of freshwater rinses, desiccation and even freezing for two days (pers. obs.)—suitable attributes for survival in an exposed habitat. Few other studies have sampled the meiofauna amongst barnacles, but a previously unrecognised species of halaearid mite was found to be widespread and common in the British Isles following the work of Bartsch (1975; cited in Somerfield & Jeal 1996), whose samples included intertidal barnacles as habitat for the Acari.

The composition of the meiofaunal assemblage on algae-bearing pneumatophores showed greater evenness and diversity than from within either of the other two habitats. Studies in New Zealand by Hicks (1986) showed that species richness of copepods on seagrass blades was nearly twice as high as on sedimentary substrata. Even relatively imperceptible and ephemeral structures such as mucous tubes have been shown by Peachey & Bell (1997) to affect the density and behaviour of epiphytic meiofauna on seagrass blades; the presence of mucous tubes constructed by a harpacticoid copepod was shown to enhance immigration rates of meiofauna onto experimental glass substrata.

The significance of surficial physical structure for small organisms is also appreciated by larval biologists, and the sensitivity of potential settlers to contours, textures and chemical signals has been investigated over many years (eg. Knight-Jones 1953; Crisp 1974; Keough & Raimondi 1995). It would not be surprising to find that mangrove-dwelling meiofauna are receptive to a similar range of stimuli from their habitat. Meiofauna have been observed to aggregate in areas where potential food (bacteria, diatoms) is concentrated (Gerlach 1977; Hogue & Miller 1981; Gerlach 1977) and the differential attractiveness of certain sediments to colonising meiofauna was demonstrated in some of the earliest experimental studies on these small animals (eg. Gray 1966). The nature of the biofilms upon the surfaces of algal fronds, filaments or barnacles may be as distinctive as the assemblages of meiofauna from these microhabitats. The 'signals' from these biofilms could elicit behavioural responses which may at least partly explain the discrete assemblages of a predictable composition in a hydrodynamic environment.

#### ACKNOWLEDGEMENTS

Funding was provided by the School of Ecology & Environment, Deakin University. I thank Dr Peter Fairweather, my principal supervisor, for help and guidance during preparation of this manuscript. I appreciate many helpful suggestions and improvements offered by Dr John Aberton, and I am grateful to Hannah Gwyther who cheerfully assisted with fieldwork in very muddy conditions. This paper forms part of my candidature for the degree of PhD within the School of Ecology & Environment, Deakin University, Victoria.

#### REFERENCES

- ALONGI, D. M., 1987a. Microbial-meiofaunal inter-relationships in some tropical intertidal sediments. *Journal of Marine Research* 46: 349–365.
- ALONGI, D. M., 1987b. The influence of mangrove derived tannins on intertidal meiobenthos in tropical estuaries. *Oecologia (Berlin)* 71: 537–540.
- ALONGI, D. M., 1990. Intertidal zonation and seasonality of meiobenthos in tropical mangrove estuaries. *Marine Biology* 95: 447–458.
- ALONGI, D. & CHRISTOFFERSEN, P., 1992. Benthic infauna and organism-sediment relations in a shallow, tropical coastal area: influence of outwelled mangrove detritus and physical disturbance. *Marine Ecology Progress Series* 81: 229–245.



- BELL, S., WALTERS, K. & KERN, J., 1984. Meiofauna from seagrass habitats: A review and prospectus for future research. *Estuaries* 7: 331–338.
- CLARKE, K. R., 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–143.
- CLARKE, K. R. & GREEN, R. H., 1988. Statistical design and analysis for a 'biological effects' study. *Marine Ecology Progress Series* 46: 213–226.
- CLARKE, K. R. & WARWICK, R. M., 1994. *Changes in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Natural Environment Research Council, Plymouth Marine Laboratory, Plymouth, U.K., 144 pp.
- CRISP, D., 1974. Factors influencing the settlement of marine invertebrate larvae. Ch. 5. In *Perspectives in Chemoreception*, Grant & Mackie, eds, Academic Press, 177–265.
- DYE, A. H., 1983. Composition and seasonal fluctuation of meiofauna in a southern African mangrove estuary. *Marine Biology* 73: 165–170.
- GEE, M. J. & SOMERFIELD, P. J., 1997. Do mangrove diversity and leaf litter decay promote meiofaunal diversity? *Journal of Experimental Marine Biology & Ecology* 218: 13–33.
- GEE, J. & WARWICK, R. M., 1994. Metazoan community structure in relation to the fractal dimensions of marine macroalgae. *Marine Ecology Progress Series* 103(1–2): 141–150.
- GERLACH, S., 1977. Attraction of decaying organisms as a possible cause for distribution of nematodes in a Bermuda beach. *Ophelia* 6: 151–166.
- GOLDIN, Q., MISHRA, V., ULLAL, V., ATHALYE, R. P. & GOKHALE, K. S., 1996. Meiobenthos of mangrove mudflats from shallow region of Thane Creek, central west coast of India. *Indian Journal of Marine Sciences* 25: 137–141.
- GOTELLI, N. & GRAVES, G., 1996. *Null Models in Ecology*. Smithsonian Institution Press, Washington, 368 pp.
- GOTELLI, N. J. & ENTSINGER, G. L., 1997. EcoSim: Null models software for ecology. Version 1.0. Kersey-Bear Inc.
- GRAY, J., 1966. The attractive factors of intertidal sands to *Protodrilus symbioticus* Giard. *Journal of the Marine Biological Association of the United Kingdom* 46: 627–645.
- HICKS, G. R. F., 1985. In *The Ecology of Rocky Coasts*, P. G. Moore & R. Seed, eds, Hodder & Stoughton, London, 36–56.
- HICKS, G. R. F., 1986. Distribution and behaviour of meiofaunal copepods inside and outside seagrass beds. *Marine Ecology Progress Series* 81: 159–170.
- HODDA, M., 1990. Variation in estuarine littoral nematode populations over three spatial scales. *Estuarine, Coastal & Shelf Science* 30: 325–340.
- HODDA, M. & NICHOLAS, W. L., 1985. Meiofauna associated with mangroves in the Hunter River estuary and Fullerton Cove, south-eastern Australia. *Australian Journal of Marine & Freshwater Research* 36: 41–50.
- HODDA, M. & NICHOLAS, W. L., 1986. Temporal changes in littoral meiofauna from the Hunter River estuary. *Australian Journal of Marine & Freshwater Research* 37: 729–741.
- HOGUE, E. & MILLER, C., 1981. Effects of sediment microtopography on small-scale spatial distributions of meiobenthic nematodes. *Journal of Experimental Marine Biology & Ecology* 53: 181–191.
- HULL, S. L., 1997. Seasonal changes in diversity and abundance of ostracods on four species of intertidal algae with differing structural complexity. *Marine Ecology Progress Series* 161: 71–82.
- JARVIS, S. C. & SEED, R., 1996. The meiofauna of *Ascophyllum nodosum*—characteristics of assemblages associated with two common epiphytes. *Journal of Experimental Marine Biology & Ecology* 199: 249–267.
- JENSEN, P., 1981. Phytochemical sensitivity and swimming behaviour of the free-living marine nematode *Chromadorita tenuis*. *Marine Ecology Progress Series* 4: 203–206.
- JENSEN, P., 1984. Ecology of benthic and epiphytic nematodes in brackish waters. *Hydrobiologia* 108: 201–217.
- KEOUGH, M. & RAIMONDI, P., 1995. Responses of settling invertebrate larvae to bioorganic films: effects of different types of films. *Journal of Experimental Marine Biology & Ecology* 185: 235–253.
- KITO, K., 1982. Phytal marine nematode assemblage on *Sargassum multicum* Agardh, with reference to the structure and seasonal fluctuations. *Journal of the Faculty of Science, Hokkaido University, Series VI (Zoology)* 23: 143–161.
- KNIGHT-JONES, E., 1953. Laboratory experiments on gregariousness during settling in *Balanus balanoides* and other barnacles. *Journal of Experimental Biology* 30: 584–598.
- NICHOLAS, W. L., ELEK, J. A., STEWART, A. C. & MARPLES, T. G., 1991. The nematode fauna of a temperate Australian mangrove mudflat—its population density, diversity and distribution. *Hydrobiologia* 209: 13–28.
- PEACHEY, R. L. & BELL, S. S., 1997. The effects of mucous tubes on the distribution, behaviour and recruitment of seagrass meiofauna. *Journal of Experimental Marine Biology & Ecology* 209.
- RAO, G., 1986. Meiofauna of the mangrove sediments in South Andaman. *Journal of the Andaman Science Association* 2: 23–32.
- RUDNICK, D. T., ELMGREN, R. & FRITHSEN, J. B., 1985. Meiofaunal prominence and benthic seasonality in a coastal marine ecosystem. *Oecologia (Berlin)* 67: 157–168.
- RUTLEDGE, P. A. & FLEEGER, J. W., 1993. Abundance and seasonality of meiofauna, including harpacticoid copepod species, associated with stems of the salt-marsh cord grass, *Spartina alterniflora*. *Estuaries* 16: 760–768.
- SCHRIVERS, J., VAN GANSBEKE, D. & VINCX, M., 1995. Macrobenthic infauna of mangroves and surrounding beaches at Gazi Bay, Kenya. *Hydrobiologia* 306: 53–66.



- SMITH, W. & GRASSLE, F., 1977. Sampling properties of a family of diversity measures. *Biometrics* 33: 283–292.
- SOMERFIELD, P., GEE, M. J. & ARYUTHAKA, C., 1998. Meiofaunal communities in a Malaysian mangrove forest. *Journal of the Marine Biological Association of the United Kingdom* 78: 1–16.
- SOMERFIELD, P. J. & JEAL, F., 1996. The distribution of halacaridae (Acari: Prostigmata) among macroalgae on sheltered rocky shores. *Journal of the Marine Biological Association of the United Kingdom* 76: 251–254.
- UNDERWOOD, A. J., 1997. *Experiments in Ecology*. Cambridge University Press, 504 pp.

Manuscript received 12 May 2000

Revision accepted 4 September 2000